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THE MALTHUSIAN PRINCIPLE AND NATURAL SELECTION

IN the last edition of his essay on population, page 2, Malthus laid down the following biological proposition from which he derived his well-known sociological conclusion:

> The cause to which I allude is the constant tendency in all animated life to increase beyond the nourishment prepared for it.
>
> It is incontrovertibly true that *there is no bound to the prolific plants and animals, but what is made by their crowding* and interfering with each others' means of subsistence. (Italics mine.)
>
> In plants and irrational animals, the view of the subject is simple. They are all impelled by a powerful instinct to the increase of their species; and this instinct is interrupted by no doubts about providing for their offspring. Wherever, therefore, there is liberty, the power of increase is exerted; and the superabundant effects are repressed afterwards by want of room and nourishment.

The great influence of this book upon Darwin is well known and so it is not surprising to find him writing in the "Origin of Species," page 60,

> A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase.

And again on page 72,

> Each organic being is striving to increase in geometrical ratio; each, at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life and to suffer great destruction.

It is quite natural, therefore, to find that in the current texts and in the class room, that natural selection is taught as starting from the contrast of a limited subsistence and a very large birth-rate (and I confess that I have been guilty). So strong an impression is thus made, that to most people, and unfortunately many sociologists, natural selection has come to mean that factor of evolution which is caused by an excessive birth rate.

The fact is frequently lost sight of that natural selection effects its results by differential success in mating (sexual selection), and differential fecundity (fecundal selection), as well as by a differential age at death (lethal selection). Even when we confine our attention to lethal selection, we shall see that a very large share of its action is in no way dependent upon the adequacy of the food supply. Such selection may well be called non-sustentative selection to distinguish it from that which is so dependent.

Sustentative selection is generally thought to be nearly always in operation. In every group of animals in which I have made any special field observations, namely, bryozoa, birds and beetles, the falsity of this belief has been impressed upon me. With fresh-water bryozoa the food supply can scarcely ever be taxed. The limiting conditions seem to be largely inconstancy of the bodies of water, the danger of being eaten, and the limited extent of suitable substrata.

With birds, when one really sees an emaciated individual, the result of some accident which has made it difficult for it to obtain food, one is struck by the very great contrast with other birds. In my experience, in skinning birds in the state of Washington, summer and winter, I never opened one not well equipped with abdominal fat. On the other hand, the great loss of the young birds by adverse weather and the large variety of predaceous enemies is common knowledge.

With lady beetles there is a more direct relation of the numbers to food supply, but even here it is a question of finding food, rather than any real lack of it. The food supply of the adult beetles, embracing aphids, pollen and spores, is superabundant. The principal causes of death seem to me to be due to inability of the females to distribute the eggs proportionately to the distribution of aphids, and, secondly, the unreliableness of aphid stocks, owing to their rapid annihilation when one of the numerous aphid diseases or parasites becomes rampant. One may often hunt over many colonies of aphids without finding any coccinellid larvæ, and then at last find one of the same species with several large egg masses. So many larvæ will hatch in this case that they will consume all the aphids before they themselves have all become mature. As a result, they will wander, only a few surviving who may have the efficient instincts and good fortune necessary to discover another stock of aphids.

Of the half dozen or so species of the large coccinellids most common in the United States, it is common to find here one species abundant, and there another, though some others are also found. Attempts to account for these contrasts in numbers on grounds of temperature, humidity, altitude and the like, have proved unsuccessful. I think it is because the instincts of egg-laying and of migration of the larvæ of one species or another is better adapted to the species of aphids and aphid-affected plants in that vicinity. Evidence to this effect is seen in the fact that certain shrubs that are aphis-infected for a short time only in the early spring sustain only *Adalia bipunctata.* The wild parsnip, which becomes infected with other aphids later, sustains *Adalia bipunctata* in numbers smaller than three of its competitors. If we take the herbivorous coccinellids, we will find similarly in some places an abundance of food that they have not touched, while some other patches of suitable plants may be stripped.

In conclusion, then, we see that in the bryozoa and birds, sustentative selection does not play the dominant rôle imputed to it. In the lady beetles, where the supply of food is seen to limit their numbers, it is not because there is not food enough, but because the individuals are not properly distributed with reference to that food. The sustentative selection in this case must be differentiated as indirect. The evolutionary significance lies in the fact that where the sustentative selection is indirect, the species may become more abundant through variations which adjust the individuals better to the food supply.

I believe there is a fundamental reason for this subordination of sustentative selection. The reproductive rate is not merely an arbitrarily large number, which necessarily causes a severe struggle, but is just such a number as is best adapted, in general, to the needs of the species. The extreme members of that school which emphasizes the importance of the variations at the expense of selection can scarcely object to this, for fecundity is always variable and these differences are known to be inheritable in many cases.

Now the number of progeny which is best adapted to the needs of the species is that number which is large enough to sustain the losses from all non-sustentative causes of death, but not large enough to invoke death by starvation. Such a species is obviously less liable to extermination than one in which the hostile influence of underfeeding always handicaps. If grasshoppers conformed to the Malthusian conceptions of many evolutionists, there should be no alfalfa, for that favorite food would all be eaten up before it could be harvested. The world teems with herbivorous animals of one kind or another, and yet also teems with plants, most of which are eaten by many species of animals. I can see no other explanation than that the species are not ordinarily subject to sustentative selection, and that when it is, it is generally the indirect selection rather than the direct.

Indirect sustentative selection is less injurious to a species, because those individuals which do become well placed thrive. The burden of starvation passes by a number of the individuals to fall upon the others. In this way, the evil effects of a general underfeeding, which is the necessary result of direct sustentative selection, is avoided. In cases, then, where indirect sustentative selection is operative, the reproductive rate is that which will produce enough individuals to find many of the favored places and withstand the non-sustentative causes of death. Where direct sustentative selection might be theoretically expected, as in the case of the large birds of prey, in regions where they are not persecuted, the rigors of a possible struggle are avoided by low reproductive rates.

While the reproductive rate must be looked upon as a characteristic which has its adaptations like other characteristics, it has one peculiarity—its increase is always opposed by lethal selection. The chances of life are reduced by reproducing inasmuch as more danger is entailed by the extra activities of courtship, and later, of the care of the young, since they reduce the normal wariness of individual life. The species, therefore, always keeps the reproductive rate at the lowest point which will suffice for the reproductive needs of the species. For this reason alone we should expect the non-sustentative selection to be the predominant kind.

Gulick and Pearson have shown that there is a normal conflict between natural selection and fecundal selection. Fecundal selection is said by them to be constantly tending to increase the reproductive ratio, while lethal selection asserts its power to reduce it, because the reproductive demands on the parents reduce their chances of life by interference with their natural ability of self-protection. This is quite true, but the analysis is incomplete, for an increased number of progeny not only decreases the life chances of the parents, but also of the young, by reducing their endowment and care.

A further reason for believing in the predominance of non-sustentative selection is the fact that the species that have evolved furthest are well known to be of low fecundity. Man, himself, even where there is no artificial restraint, has one of the smallest reproductive rates known. If sustentative selection had been predominant, we should expect higher fecundities in these highly evolved species than in the lower ones.

The fundamental formula of Malthusianism, that the number of individuals in a species tends to increase in geometrical ratio, is misleading, and a great mass of biological and sociological writing has been led into error by it. Of course, there can be no objection to the position that since the number of progeny exceeds the number of parents, there must be many premature deaths, or the species will increase in numbers. But this is a truism. The real essence of Malthusianism lies in the conclusion that a sustentative struggle must arise, and there lies the error. The Malthusian conception of the rate of reproduction is that the rate is such that the food supply must be overtaxed and a struggle for existence will take place. The conception here urged is that each species has such a reproduction rate as will suffice to withstand the premature deaths and sterility of some individuals, and yet not so large as to press normally upon the limits of the food supply.

I believe the common over-estimation of the rôle of sustentative selection, and the neglect of the non-sustentative, is largely historical in origin, and that it is maintained by improper teaching.

In teaching natural selection, the fault is generally made of starting with the Malthusian contrast between the limitation of the food supply and the rate of reproduction. The current conception will not be righted until we learn to teach natural selection more correctly. While the rate of reproduction is the proper place from which to start, this should be treated, not as a fixed quantity to which nature must accommodate itself, but as that number which just exceeds the great number of premature deaths and suffices to replace the parents. Then the premature death of the 999 must be explained. After an examination of these causes the student can not but grasp the master rôle of the non-sustentative form.

Finally, then, we see from these considerations, that the common assumption that every species is as common as it can be, because it is living up to the limits of subsistence is erroneous. A relaxation of any of the causes of death in most cases will increase the numbers.

[This article was written while the author was on the staff of the Station for Experimental Evolution at Cold Spring Harbor, N. Y., of the Carnegie Institution of Washington.]

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